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AN AGE DIFFERENTIAL OF MIGRANTS IN COASTAL CALIFORNIA

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While the age distribution and species composition of North American avian breeding populations is reasonably well known, comparable information is generally not available on migrating populations. Capture data taken at the Point Reyes Bird Observatory on the coast at Bolinas, 23 km NW of San Francisco, and at other stations in California have provided information on the composition, seasonal timing, and relative abundance of various species of land bird migrants.

The data presented below concern the fall migration of three nocturnally migrating passerine species, the Warbling Vireo (*Vireo gilvus*), the Wilson's Warbler (*Wilsonia pusilla*), and the Western Flycatcher (*Empidonax difficilis*). I wish to emphasize one fact: the abnormally high percentage of young found along the coast in fall migration. I feel that a majority of these young birds are not adapted for successful migration. A study of these individuals might reveal the relative importance of the various adaptations for migration, and thus the causes of mortality during this critical period.

These species have been chosen for analysis because of their abundance during both migration and breeding at Point Reyes, and because their wintering grounds are in the tropics. This latter fact ensures that the birds captured are long distance migrants, and are thus subjected to the maximal selection induced by migration. On the mainland the birds analyzed in this study were captured entirely by mist nets, while on the Farallon Islands, 25 km W of the Observatory, a Heligoland trap was also used. Age was determined by the extent of skull ossification and by plumage characteristics, criteria felt to be accurate in more than 95 per cent of individuals examined.

THE WARBLING VIREO AT POINT REYES

A brief summary of the annual cycle of the Warbling Vireo in the Point Reyes area, is reasonably represent-

ative of all three species and will give perspective to the following data. The summer residents at Point Reyes generally arrive during March (fig. 1A), and by April are nesting. Migrants breeding farther north pass through in peak numbers during the latter part of April and the first part of May (fig. 1B). This late influx is synchronous with the arrival of this species on the Farallon Islands (fig. 1C), where there is no breeding population. The majority of Point Reyes adults leave during July and early August, and may be in full migration (but see below). At this time there is an increase in young birds (fig. 1B), probably representing dispersal of locally produced young.

The evidence available indicates that fall migration begins after 1 August and continues through October, and this period was used in calculations. The first fall migrants of this species were recorded on 6 August at San Diego (Alan and Jean Craig, pers. comm.) at the extreme southern limit of breeding of the subspecies *V. g. swainsonii*. The species was first noted on the Farallon Islands on 29 August.

AGE RATIO OF MIGRANTS

During the fall migration period described, virtually all Warbling Vireos captured are young (table 1). The adult:young ratio is 1:19, far too high for the normal age distribution of 1:1 to 1:4 (expected on the basis of normal clutch size and survival of young). Similarly, captures of the Wilson's Warbler and Western Flycatcher show even higher age ratios during the fall migration (1:28 and 1:26). These disproportionate ratios indicate either that the adults in all three species produced between 38 and 56 young per pair, or that an additional factor(s) is influencing the occurrence of these species on the coast of central California. Note that the age ratio of all three species is even more disproportionate on the Farallon Islands than on the adjacent mainland, the difference being significant at the 0.05 level. This very high proportion of young in fall migration is found in all species of nocturnal passerine migrants in this area (Ralph, unpubl. data), and can thus be considered a general phenomenon, although the specific causes may vary in each species.

HYPOTHESES ADVANCED TO EXPLAIN AGE DIFFERENTIAL

The great preponderance of young of nocturnal migrants in coastal situations has long been recognized

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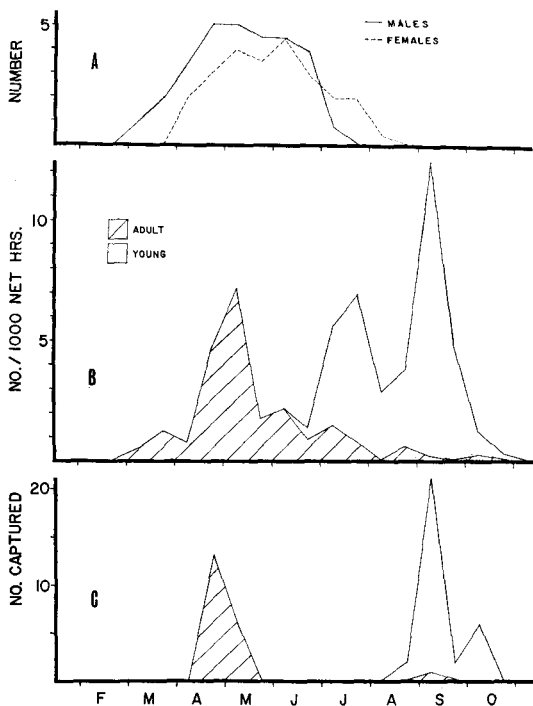


FIGURE 1. A. Mean number of breeding Warbling Vireos in a six-acre plot at Bolinas, California, 1967-1968. B. Number of Warbling Vireos captured at Bolinas, California, per 1000 net hr (a 12 m net in operation for 1 hr) during 1967 and 1968. C. Number of Warbling Vireos captured on South Farallon Island, California, during 1968.

(Robbins et al. 1959). Although this phenomenon apparently has been demonstrated on the coast of Britain (e.g., Williamson 1959; Evans 1968), it has been adequately documented only on the Atlantic coast of the United States. The data presented above are the first from the Pacific coast. Samples taken farther inland generally reveal lower proportions of young, usually 40-60 per cent (e.g., Nisbet et al. 1963; Leberman and Clench 1969).

Evidence from a great variety of literature sources (including data from direct observations, laboratory experiments, telemetry, and radar) indicate the following as the probable sequence of events in the flight of a nocturnal passerine migrant. The flight, begun at dusk, is in a constant direction, and continues to be so through the night. The guidance results from primarily celestial cues until dawn or somewhat before, when these birds begin to descend and seek land. If their innate navigational tendency has taken them over water, they attempt to return to the mainland and probably succeed if it is within sight.

The difference between the normal age ratios of migrants inland, and the disproportionate ones of those birds along the coast might occur from any of three causes: (1) an abnormally small number of adults, and a normal number of immatures; (2) a normal number of adults and an abnormally large number of immatures; or (3) a virtual lack of adults and a small number of immatures, the vast majority of adults and immatures taking routes that do not bring them near the coast. As discussed below, this last alternative seems the most likely.

TABLE 1. Age composition of fall migrants captured at Point Reyes (1967-68), and on the Farallon Islands (1968-69), California, 1 August-31 October.

Species and site	Adults n	Adults %	Young n	Young %	Total
Warbling Vireo					
Point Reyes	5	5.9	80	94.1	85
Farallon Islands	1	3.0	32	97.0	33
Total	6	5.1	112	94.9	118
				(Ratio of 1:19)	
Wilson's Warbler					
Point Reyes	4	5.4	70	94.6	74
Farallon Islands	1	1.4	72	98.6	73
Total	5	3.4	142	96.6	147
				(Ratio of 1:28)	
Western Flycatcher					
Point Reyes	10	4.3	220	95.7	230
Farallon Islands	0	0.0	35	100.0	35
Total	10	3.8	255	96.2	265
				(Ratio of 1:26)	

The five principal hypotheses that have been advanced to explain the phenomenon largely concern migration along the Atlantic coast of New England, where apparently two groups of nocturnally migrating passerine birds occur (Drury and Keith 1962). One group, comprising the majority of migrants, maintains a general southwesterly route, keeping the birds over land. The remainder (probably fewer than 10 species), move southward on a route that takes them directly overwater to the Lesser Antilles and South America. (On the Pacific coast no such overwater route exists, and all migrants move southeast, which corresponds to the southwesterly migrants of the Atlantic coast.)

Southerly migrating species. In relation to those few species that normally migrate south overwater to South America two hypotheses have been advanced to explain the phenomenon:

(1) Drury and Keith (1962) hypothesized that "the concentration of immatures resulted from their indecision while adults unhesitatingly strike out across the water." However, the species involved are nocturnal migrants, a fact which at least reduces the probability that the birds are aware of the change in the landscape below. Even if true for these few species, radar studies show that most nocturnal passerine migrants in New England avoid the coastal areas and head southwest overland (Drury and Nisbet 1964). Since most passerines, and certainly those adults on at least their second fall migration, do not normally come near the coast, other explanations should be sought for the movements of the majority of species.

(2) Murray (1966), on the other hand, suggested that as the migrating flocks return to the coast in the morning after finding themselves offshore at dawn, the immatures might stop at the first landfall, while the adults more frequently move further inland. This assumes, as does alternative (1), that both adults and young of most species regularly make flights over the ocean, and thus is open to the same objections. The assumption that the immatures flying over the ocean might survive to become adults seems rather unlikely.

While there is no direct evidence from the east coast to disprove these hypotheses, they certainly do

not explain the similar situation on the Pacific coast where there is no destination for any passerine birds migrating south overwater.

Southwesterly and southeasterly migrating species. The maintenance of normal overland migratory direction, southwest on the Atlantic coast and southeast on the Pacific coast, which involves the majority of species, may be similarly explained and three additional hypotheses have been advanced for these species:

(3) One explanation of the coastal-inland age differential for these species does not assume synchronous migration, but rather postulates that post-breeding adults migrate in July before the young (Brewster 1887). If this is so, few adults would occur along the coast during migration because most of them are already well to the south after August. There is evidence for early migration of adults in some species, e.g., the Least Flycatcher, *Empidonax minimus* (Hussell et al. 1967; Ely 1970). However, if the California post-breeding adults of any species are migrating significantly earlier than the young, they are probably not doing so at night in the 300–400 km flights of normal migration. This can be inferred from four lines of evidence:

(a) In the vicinity of the Observatory at least a few members of the local population of breeding adults (less than 10 per cent) have been captured at least through late August.

(b) No adults of the three species mentioned above have been recorded on the Farallon Islands or in San Diego in any numbers before September. If migration were occurring prior to September, a few individuals would be expected in these localities. Even if this is not the case, and the adults are in fact migrating early, they are at least avoiding the coast. Unless one can subscribe to the unlikely idea that a bird in his second fall migration takes a different route and/or longer migration flights than he did in his first migration, selection must have occurred to eliminate those birds whose route took them near the coast.

(c) In an extremely well-documented study of the Hammond's Flycatcher (*Empidonax hammondi*), Johnson (1970) found no age differential in timing of migration. This study covered the entire migration range of the species, and thus avoided the pitfalls of more localized studies.

(d) In the specific case of the Least Flycatchers, Clench (1969) has pointed out that the migration of adults in Pennsylvania, which is in their breeding range, takes place a full month later than observed by Hussell et al. (1967) and Ely (1970), and is in synchrony with migration of the young. Hussell et al. worked in Ontario only 275 km NNW of Clench, but 30 or more km from the nearest breeding habitat, while Ely was situated in Kansas slightly to the south of their breeding range and on the western part of their migration route. I suggest that Clench observed the results of normal nocturnal migration, while, in contrast, Hussell et al. and Ely observed post-breeding dispersal. It seems likely that once breeding is terminated the adults leave their nesting area, but do not migrate. They may even move in the normal migratory direction. Later, during the autumn, they begin the normal long nocturnal flights at the same time as the immatures. This explanation accounts for the paucity of adults along the coast during migration per se.

(4) Drury and Keith (1962) proposed that the paucity of adults was due to the young having learned by individual experience to avoid the coast and fly on inland routes. This presumes that many birds in their first fall migration meet the hazards of overwater flight

and learn from this experience. Those that do not learn, perish at sea when energy stores are exhausted. Each generation learning anew seems highly unlikely, and a more likely explanation is that a genetic encoding determines proper orientation. As an alternative, young birds could learn the correct route from the adults in their flock, but this is impossible to demonstrate. Our knowledge of the ability of young birds to orient in the proper migratory direction in cages before having any migratory experience (Emlen 1969) also makes this explanation unlikely.

(5) Drury and Keith (1962) also suggested that "the birds which live to be adults are those inheriting a tendency to move on courses which keep them over the mainland." These birds would either be ones having adequate orientation, adequate compensation for wind drift (Baird and Nisbet 1960), and/or ones who begin migration only under those weather conditions which will not lead to wind displacement from the species' normal route (Evans 1968). The birds along the coast would thus be largely immature birds who had not inherited these abilities, thus exposing themselves to the hazards of overwater flight.

DISCUSSION

Although the first four hypotheses may be at least partially valid, and account for a small percentage of the young on the coast, the fifth seems the most likely explanation for the occurrence of most of these young birds on the Pacific coast. All three of the California species discussed above winter primarily in tropical areas of southern México and Central America. To arrive in those areas, the nocturnal migrants from northern California, Oregon, and Washington are obliged, simply by the southeasterly inclination of the west coast of the Americas, to travel southeastward during the fall migration. Birds whose navigational tendencies take them in a more southerly direction would soon find themselves over the Pacific Ocean and would be eliminated from the population if unable to return to land. Those able to return to land would comprise the bulk of the coastal population of migrants. An increase in the percentage of young between the mainland and offshore station (discussed above) corroborates this. The farther from the mainland, the greater the percentage of young to be expected.

I therefore subscribe to the postulate of Drury and Keith that the preponderance of young birds along the coast is due in large part to various genetically-induced navigational errors, and that the vast majority of migrants take inland routes. This seems most likely to be the case along the Pacific coast and probably on the Atlantic coast of the United States and Europe. Deviation from a strict inland route in either of the latter coasts may have less significance in that the migrants have proportionally larger target areas.

SUMMARY

Age composition differing significantly from the normal was demonstrated for three species of autumnal, long distance nocturnal passerine migrants on the central California coast. Approximately 95 per cent of the individuals captured were young birds. Of the various explanations proposed to explain this phenomenon, the most likely interpretation is that the immatures along the coast are individuals who possess genetically-based navigational tendencies of a non-adaptive sort. Not only are such birds removed from their normal migratory route, but they are also exposed to the hazards of an overwater flight.

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EXPLOITATION OF NECTAR RESOURCES BY HUMMINGBIRDS, BEES (*BOMBUS*), AND *DIGLOSSA BARITULA* AND ITS ROLE IN THE EVOLUTION OF *PENSTEMON KUNTHII*

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The negative effect of illegitimate nectar foraging (i.e., obtaining nectar in a fashion other than that "intended" by the morphology of the blossom) on successful pollination is reflected in various generalizations concerning pollination syndromes. For example, hummingbird flowers have long narrow tubular flowers which to a greater or lesser degree discourage hymenopterous visitors. It is assumed, perhaps a priori, that illegitimate foraging will result in fewer legitimate visits and hence a lowered number of successful pollinations. Below, we present our observations and discuss the possibility that illegitimate visitation may have a positive rather than negative effect on the evolution of a bird flower. Specifically, our study is concerned with the possible effect the flower-piercer (*Diglossa baritula*) and bumblebees (*Bombus pulcher* and *B. trinommatatus*) have had on the evolution of the hummingbird pollinated *Penstemon kunthii*.

Under certain circumstances both insects and birds forage for nectar in such a manner that pollination is not effected. Often this involves various physical mis-fittings between flower and visitor such that, even

though foraging is legitimate, pollination does not occur. Thus small bees and hummingbirds, for example, may visit flowers structurally adapted for pollination by large bees and obtain nectar, yet fail to contact the flowers' anthers or stigmas. Illegitimate foraging rarely if ever results in pollination. Bumblebees (*Bombus*) were early observed to perforate the nectar spurs of *Aquilegia* (Sprenzel 1793) and such observations have frequently been made since that time (Macior 1966, etc.). Hummingbirds also secure nectar in a similar fashion (Skutch 1954).

In some cases the perforators are followed by "gleaners," e.g., corolla perforations made by *Bombus* in *Aquilegia* are later utilized by *Apis* and *Lasloglossum* for securing nectar (Macior 1966). However, in such situations little attempt has been made to determine what effects, if any, the opportunity for additional nectar exploitation has had on populations of the secondary user, or on the floral evolution of the exploited plant species. In 1968, during the course of investigations of hummingbird ecology on Cerro San Felipe in the Sierra Madre de Oaxaca northeast of the city of Oaxaca, México, we observed a bird-bee interaction involving the Cinnamon-bellied or Slaty Flower-piercer (*Diglossa baritula*) and two species of bumblebees, *Bombus pulcher* and *Bombus trinommatatus*. In this case the perforator was *Diglossa* and the "gleaners" were bumblebees. Our observations are recorded here in an attempt to shed light on some of these bird-bee population interactions, especially the possible effect usage by *Diglossa* may have had on the evolution of *P. kunthii*.

OBSERVATIONS

Starting in mid-June and continuing into October, *P. kunthii* flowers profusely in mountain meadows of the Sierra Madre de Oaxaca and is a primary nectar